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Post-establishment fertilization of Minnesota hybrid poplar plantations

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Abstract

Experimental plantings were installed at five sites in three locations in western Minnesota. Aboveground biomass production increased 43–82% as a result of three annual applications of urea or balanced nutrient blend fertilizer beginning near canopy closure. There were no production differences between the type of fertilizer used, indicating that N was the major limiting nutrient. Responses were consistent from site to site, indicating that hybrid poplar stands in this region at this stage of development would be very responsive to fertilization. Leaf tissue N, P, and K concentrations increased in response to both fertilizer treatments; P and K increased more frequently in response to the blend treatment compared to the N-only urea treatment. The diagnosis and recommendation integrated system (DRIS) indices indicated that the stands were near optimal nutritional balance prior to fertilization. Treatments increased individual leaf area and leaf litter production up to 33% and 37%, respectively. Canopy leaf area, leaf N concentration and the sum of DRIS indices were correlated with aboveground production. Growth efficiency, the ratio of production to canopy leaf area, increased with both fertilizer treatment and successive years of treatment, indicating improved stand vigor due to nutrient amendments. Stand production increased more in response to changes in leaf N concentration as stands aged. Plantation production continued to increase with increased internal N concentration even when deficiency levels or levels defined as sufficient for fast growth were exceeded. The correlation between aboveground production and the sum of DRIS indices shows that optimal nutrition at canopy closure may result in current aboveground dry matter production exceeding 13 $Mg\,ha^{-1}\,yr^{-1}$. Multiple small-dose amendments appear to be effective in increasing production by maintaining high internal N concentrations.
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Keywords: Biomass; DRIS; Forest tent caterpillar; Growth efficiency; Nutrient addition rate; Optimal nutrition; Short rotation woody crops; Urea

1. Introduction

Fertilization of non-irrigated poplar plantations typically occurs at the time of site preparation or near the time of canopy closure [1]. Fertilization at canopy closure is usually preferred because it does not cause excessive growth of herbaceous weed competition, because it provides nutrients to poplar trees at a stage of critical need, and because it shortens the period during which the expense is discounted [1,2]. Fertilizer application can increase productivity from 20% to 60% or more depending on the site's capacity to supply required nutrients [3–8]. However, production on some sites responds little if at all to fertilizer amendments.

Techniques for identifying plantations that will respond to nutrient additions have advanced little over the last decade. Dickmann and Stuart [2] defined nitrogen (N) deficiency to be leaf concentrations below 20 $mg\,g^{-1}$. Hansen [9] recommended maintaining mid-season concentrations of N in upper canopy foliage at or above 30 $mg\,g^{-1}$. Yet greenhouse and field data show that when nutrients are applied in regular small doses designed to match nutrient demand, growth is positively correlated

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with leaf N content beyond the 20 mg g^{-1} deficiency level and even the 30 mg g^{-1} sufficiency level [10,11]. Current diagnostic methods are based on the assumption that there is a threshold response; however, if the response is linear, amendments can be justified even above critical leaf nutrient concentrations. Clearly, greater precision is required in the diagnosis of poplar fertilizer requirements.

Improved diagnostic precision should include measuring concentrations of various nutrients in addition to N. Although N is the main nutrient limiting growth in poplar [1,12], the balance among all nutrients affects the response to N fertilization. If another nutrient is deficient relative to N, or some other factor limits growth, no response to N fertilization will be realized. The DRIS (diagnosis and recommendation integrated system [13]) evaluates the balance among all nutrients based on norms for high-yielding plantations. With DRIS the ratios of multiple nutrients are used in calculating easy-to-interpret index values for each included nutrient. The sum of all DRIS indices is a measure of nutritional balance. DRIS has proved useful for nutrient diagnosis in poplar [14] and numerous other forest species [15–22].

The relationship between aboveground production and total leaf area defines stand growth efficiency and is a measure of stand vigor [23]. Stand vigor as measured by growth efficiency is related to tolerance of pest infection and fertilizer response [24–26]. It is, therefore, useful to determine the amount of leaf area maintained by trees in response to fertilization and identify levels of growth efficiency that indicate a positive response.

In this study, we tested fertilizer response in post-establishment hybrid poplar stands with foliar nutrient concentrations greater than recommended threshold levels. We applied annual amendments to match nutrient demand with the objective of maintaining favorable internal nutrient concentrations. We used DRIS to evaluate nutritional balance as affected by N-only fertilizer or a mixed fertilizer blend. Our assumption was that improved nutrient balance would be achieved or maintained by using a balanced blend and that nutrient balance would decline with continued application of N-only urea fertilizer. We also monitored leaf and canopy characteristics and calculated growth efficiency in an effort to identify alternative methods for diagnosing nutrient response through measurement of tree vigor. The aim was to apply a consistent experimental design over a variety of sites to produce adequate data for examining relationships between nutrient concentrations, leaf area and aboveground production.

2. Materials and methods

2.1. Study locations and experimental design

We compared three fertilizer treatments at five experimental sites in a network of hybrid poplar plantations near Oklee, MN. The plantations were established in 1995 and 1996 on private farmland in cooperation with Minnesota Power, University of Minnesota—Crookston, and the Agricultural Utilization Research Institute. The five experimental study sites were distributed among three locations in Red Lake County, Minnesota (95.78°W, 47.90°N). Each site had good stocking and consistent tree form (Table 1). Weed competition was low at each of the sites due to cultivation during site preparation, application of pre-emergent herbicide (Linuron[1]) just after planting, cultivation during establishment, and annual application of contact herbicide (Glyphosate) as needed. Clones selected for the study (DN17 and DN34, both *Populus deltoides* × *Populus nigra* hybrids) are commonly deployed in Minnesota. At two of the three locations, separate studies were established in adjacent clonal blocks to allow for tests of clone, location and fertilizer treatment interactions. Two soil types occurring at these locations are representative of the area. The Reiner series is a slightly acidic fine-sandy loam (frigid Oxyaquic Argiudolls). The Smiley series is a slightly alkaline sandy-clay loam (frigid Typic Argiaquolls).

There were nine treatment plots (14 × 14 tree) at each experimental location. Each treatment plot (0.12 ha) included four border rows of trees that surrounded a 36-tree measurement plot. At each of the eight experimental sites, three replicate blocks were ranked based on mean initial diameter measurements taken May, 1999. The three plots with largest initial mean aboveground diameters at breast height were grouped in one block, the three with intermediate aboveground diameters were grouped in a second block, and those with smallest aboveground diameters were grouped in a third block. Treatments were randomly assigned to plots within each block.

Fertilizer was applied annually in May of 1999, 2000 and 2001. Fertilizer treatments were (1) a non-fertilized control, (2) 50 kg N ha^{-1} of broadcast granular urea, and (3) 50 kg N ha^{-1} of a broadcast fertilizer blend. The fertilizer blend was an 18–18–18 formulation with 2.5% S blended from diammonium phosphate, urea, potash and ammonium sulfate. Ammonia N and sulfate were included to lower pH for the purpose of improving nutrient availability. Plots receiving the fertilizer blend also received a commercial micro-nutrient product (Micromax, Grace Sierra, Inc.[2]), which supplied 350 g ha^{-1} Fe, 73 g ha^{-1} Mn, 2.9 g ha^{-1} B, 15 g ha^{-1} Cu, 29 g ha^{-1} Zn, and 1.5 g ha^{-1} Mo.

[1]This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and Federal agencies before they can be recommended. *Caution*: Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

[2]The use of trade or firm names in this publication is for reader information and does not imply endorsement by the United States Department of Agriculture of any product or service.

Table 1
Stand description prior to initial treatment in 1999

Location	Clone	Age	Density[a] (trees ha^{-1})	1999 Basal area[b] ($m^2 ha^{-1}$)	Soil series	Insecticide[c]
Barth	DN17	3	1542±30	3.75±0.30	Smiley loam	+
Barth	DN34	3	1339±26	2.70±0.33	Smiley loam	+
Fore	DN17	4	1417±42	3.66±0.23	Reiner fine-sandy loam	–
Hofstad	DN17	4	1350±29	2.15±0.19	Smiley loam	–
Hofstad	DN34	4	1376±40	3.58±0.28	Smiley loam	–

[a]Stands were planted to 1682 trees ha^{-1} (2.43 × 2.43 m).
[b]Basal area includes multiple stems arising from first-year height growth increment.
[c]Foray 48B insecticide application in 2001 is indicated by "+". No insecticide application indicated by "–".

Forest tent caterpillar (*Malacosoma disstria*) was detected in Red Lake county Minnesota in mid-May of 2001. A fixed-wing aerial application of Foray 48B (Abbott Labs, active ingredient *Bacillus thuringiensis*, Bt) was made in the first week of June 2001 at the Barth location (Table 1). At that time the caterpillars had reached a length greater than 1 cm. Bt was applied to dry foliage using ultra low volume application equipment with a droplet size of 75–150 μm. The application rate was 10 billion International Units per acre (340 g without water dilution). The caterpillars discontinued eating within one day of the application and were dead within 10 days.

2.2. Growth and canopy responses

To measure tree growth, we determined the change in dry biomass for each observation year. Individual tree aboveground leafless biomass (DM, kg) was calculated from diameter (d, cm) measured 1.37 m aboveground using the following equation derived from data of Netzer et al. [27]: $DM = 0.007d^3 + 0.1058d^2 + 0.2001d$ ($R^2 = 0.9838$).

Diameter measurements were collected in May and October 1999 and in October 2000 and 2001. Each individual stem arising from the first height growth increment was treated separately. To calculate standing biomass for each plot, the DM was summed for all live trees on the plot and divided by plot area (ha). In 1999, we calculated current annual production by subtracting May standing biomass from October standing biomass for each plot. In 2000 and 2001 we subtracted previous October standing biomass from current October biomass.

We sampled foliage in mid July each year to measure nutrient concentrations and specific leaf weight. We collected a total of six recently matured leaves from branches arising in the current height-growth increment in each of three trees. Sampled leaves from each tree were divided for nutrient analysis and for measurement of specific leaf weight. Leaf samples generally came from leaf plastochron index 7–12 [28]. Foliage is routinely sampled in July to avoid errors due to annual fluctuation and to obtain repeatable nutrient concentrations [9]. We analyzed the composite sample of nine leaves per plot for essential nutrients. Foliar N concentration was determined using a dry combustion method. In addition, samples were digested using concentrated nitric acid and H_2O_2 and analyzed for total concentrations of the remaining essential plant nutrients (ICP determination). Nutrient analyses were used to calculate DRIS nutritional balance indices [13] using Leech and Kim's [14] poplar norms.

We used the remaining leaves collected from each plot to determine leaf size and specific leaf area (area per unit weight). Leaf area was measured for the nine leaves sampled. A composite dry weight was taken after oven drying to constant weight.

Litterfall collection occurred monthly at the end of the growing season. Three litter baskets (0.189 m^2) were put in place the first week of August. Collections were made from these baskets at the beginning of September, October and November. Collected samples were dried and weighed and their weight was expressed on a unit land area basis. We also converted total weight of leaves to a canopy leaf area basis by multiplying the weight of litter by the specific leaf area described above for live sampled leaves. Growth efficiency was calculated as the current annual aboveground biomass production rate divided by litterfall mass.

2.3. Data analysis

Data for aboveground biomass, current annual aboveground biomass production, nutrients, individual leaves, litterfall and growth efficiency were analyzed using repeated measures randomized block design nested within sites. The SAS MIXED procedure (SAS Institute Inc. Cary NC) was used for this purpose including treatment, site and year as fixed effects and block within site as the random effect. The purpose of this analysis was to determine if treatment, site and their interaction varied over time, therefore the interaction of these factors with year of measurement indicated significant effects. We performed multiple comparisons of means using the LSMEANS option, which adjusts comparisons using Tukey's method [29]. Covariate analysis was used to investigate the effect of year and treatment (covariates) on the relationship between total aboveground production and the independent factors of leaf N concentration and litterfall. The interaction between the covariate and the independent factors in the covariate analysis tested for slope differences among factor levels.

3. Results

3.1. Growth responses

Aboveground leafless dry biomass increased by a factor of 3.5 between May 1999 and October 2001 (Table 2). Site-to-site differences in biomass increased during that period. Despite site differences, the response to fertilizer at each site was the same (note non-significant site by treatment interaction with time in Table 3). By the end of the first year, fertilizer increased biomass by 15%. By the end of the third year, fertilizer applications resulted in more than a 40% increase in biomass. Both fertilizer treatments produced similar biomass responses. In no year did the urea treatment's effect on biomass differ from the blend treatment's effect on biomass.

Aboveground biomass production increased from 1999 to 2000, but production did not always increase between 2000 and 2001 (Fig. 1). Production declined at the Fore and Hofstad sites in 2001 where tent caterpillar infestation was not controlled. However, production did increase in 2001 at Barth where insecticide was applied to control tent caterpillars. Fertilizer treatment caused a significant increase in production at each of the study sites (Fig. 1, Table 3). Averaged across all locations, fertilizer treatments increased production 43%, 61% and 82% for years 1999, 2000 and 2001, respectively. The two types of fertilizer produced responses that were statistically equivalent ($P>0.41$). Although there were site-to-site differences in production, there were no site-by-treatment interactions, which indicates that the fertilizer response was the same at all sites.

Clones did not differ in their response to fertilizer. When we tested the clone effect on biomass and production by including the four study sites at the Barth and Hofstad locations, no clone or treatment-by-clone effect was observed ($P>0.18$). However, there were differences between clones at each location. DN17 was larger at Barth and DN34 was larger at Hofstad (Fig. 1), which was indicated by a significant site-by-clone interaction ($P<0.007$).

3.2. Nutrient concentrations

Leaf nutrient concentration changed over time and responded to fertilization (Table 4). Between the 1999 and 2001 sampling dates, average leaf N concentration, among all sites and treatments, declined 25% from 36 to 27 mg g^{-1}. Concentrations of other nutrients were frequently greatest in 2000. Fertilization caused significant increases in several nutrient elements, especially if they were included in the fertilizer treatment. Within each treatment year, fertilization increased leaf N concentration. P and K concentration increases were more commonly observed in the blend treatment. However, improved N availability in the urea treatment apparently improved uptake of other nutrients; this is indicated by increased concentrations of P, K and Fe, especially in the first years of treatment. Concentrations of several nutrients (Ca, Mg,

Table 2
Standing aboveground dry biomass for each measurement date

	Total stem biomass (Mg ha^{-1})			
	May 1999[a]	Oct 1999	Oct 2000	Oct 2001
Control	7.3 ± 0.5	11.0 ± 0.8 b[b]	16.5 ± 1.1 b	20.6 ± 1.4 b
Urea	7.7 ± 0.5	13.2 ± 1.0 a	21.8 ± 1.6 a	29.1 ± 2.0 a
Blend	7.7 ± 0.4	12.7 ± 0.9 ab	21.7 ± 1.5 a	28.8 ± 2.1 a

[a]May 99 data included for information purposes. No pretreatment differences were observed, nor were they included in repeated measures analysis.
[b]Treatment means ($n = 15$) within each year followed by the same letter are not significantly different ($P = 0.05$).

Table 3
Analysis of variance *P*-values for variables tested using a repeated measures design

Source	df	Biomass	Production	Growth efficiency	Individual leaf area	Litter
SITE	4	<.001	0.001	0.089	<.001	0.001
TRTMT	2	0.001	<.001	0.001	<.001	<.001
SITE*TRTMT	8	0.732	0.282	0.895	0.527	0.751
YEAR	2	<.001	<.001	<.001	<.001	<.001
SITE*YEAR[a]	8	<.001	<.001	<.001	<.001	0.000
TRTMT*YEAR	4	<.001	<.001	0.080	0.001	0.347
SITE*TRTMT*YEAR	16	0.813	0.835	0.835	0.206	0.500

[a]Repeated measures analysis focused on determining if treatment and site effects varied over time, therefore the interaction between these effects and time determined significance of the effect.

Mn, B, Cu, Zn, and Al) declined in the fertilizer treatments, whether or not they were included in fertilizer amendments.

DRIS indices showed that the trees were in good nutritional balance initially (Table 5). Magnesium was the only nutrient included in the analysis that exceeded the ± 10 unit range surrounding zero, which is the point of optimal nutritional balance. Nutrient indices for faster growing trees in fertilized treatments were closer to the zero balance point. The Ca index was the only exception. Improved overall balance is indicated by the lower sum of indices. Even the N-only treatment had a lower sum of indices than did the control.

The sum of DRIS indices was linearly related to aboveground production ($P<0.0001$, Fig. 2). The relationship was negative because nutritional balance decreased as the sum increased. The slope of the line did not vary from year to year ($P<0.60$), but the line shifted away from the origin with increasing age. The outward shift indicates that the maximum potential production (y-intercept) increased in successive years at this stage of stand development, and that the level of imbalance as measured by the sum of DRIS indices increased in successive years.

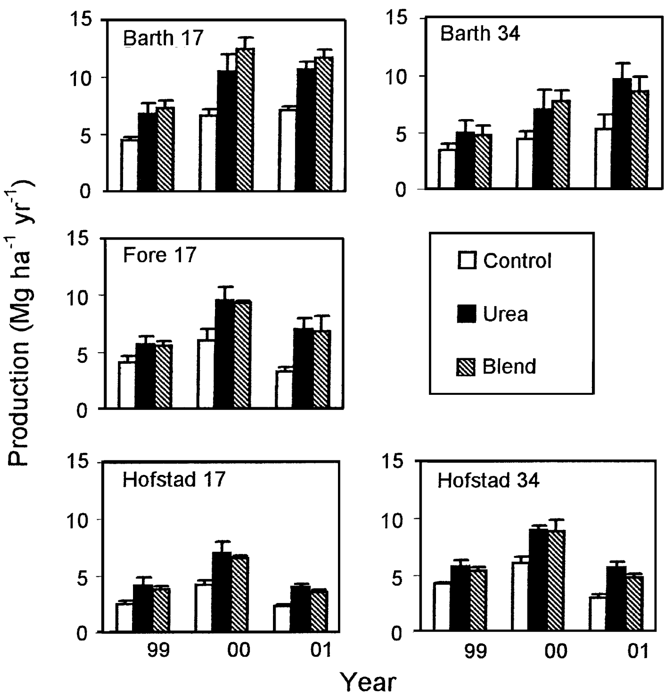

Fig. 1. Current annual aboveground biomass production for five poplar plantation experimental sites treated with fertilizer during three successive years. Study sites were distributed among three locations. Two locations contained study sites with both poplar clones DN17 and DN34. Fertilizer was applied either as urea or as a balanced fertilizer blend, each containing $50\,kg\,N\,h^{-1}\,yr^{-1}$. Each bar is the mean $\pm$se ($n=3$).

Table 5
DRIS indices for upper canopy foliage sampled during three years of treatment

	N	P	K	Ca	Mg	Sum
1999						
Control	−0.7[a] b[b]	−2.1 b	−5.8 b	−1.8 a	10.5 a	21.3[c] a
Urea	1.4 a	−0.9 a	−4.3 a	−4.0 b	7.8 b	18.7 ab
Blend	1.1 a	−0.7 a	−4.1 a	−3.8 b	7.5 b	17.4 b
2000						
Control	−8.8 b	−1.4 c	−6.7 c	0.5 a	18.1 a	36.0 a
Urea	−3.1 a	0.3 b	−4.8 b	−2.0 b	10.7 b	21.6 b
Blend	−2.6 a	1.9 a	−3.6 a	−3.2 c	9.3 b	20.6 b
2001						
Control	−6.8 b	−9.0 c	−7.7 b	0.5 a	20.5 a	45.2 a
Urea	−4.3 a	−7.6 b	−7.4 ab	−0.7 b	16.9 b	37.3 b
Blend	−4.2 a	−5.4 a	−6.5 a	−1.3 b	15.8 b	33.4 b

[a]Individual elements are considered deficient when the index value is less than −10, and supra-optimal when an index value is greater than +10.
[b]Means ($n=45$) within each year followed by the same letter are not significantly different ($P\leqslant 0.05$).
[c]The overall balance is calculated by summing the absolute values of individual indices. Greater balance is indicated by lower sums.

Table 4
Leaf nutrient concentration for upper canopy foliage sampled during three years of treatment

	N ($mg\,g^{-1}$)	P ($mg\,g^{-1}$)	K ($mg\,g^{-1}$)	Ca ($mg\,g^{-1}$)	Mg ($mg\,g^{-1}$)	S ($mg\,g^{-1}$)	Fe ($\mu g\,g^{-1}$)	Mn ($\mu g\,g^{-1}$)	B ($\mu g\,g^{-1}$)	Cu ($\mu g\,g^{-1}$)	Zn ($\mu g\,g^{-1}$)	Al ($\mu g\,g^{-1}$)
1999												
Control	32.8 b[a]	4.2 b	17.2 b	8.9 a	3.4 a	3.2 b	49.5 b	23.6 a	29.5 a	8.6 b	63.5 a	
Urea	37.0 a	4.7 a	18.6 a	7.5 b	3.1 b	3.3 b	54.0 a	22.0 a	28.4 a	9.7 a	64.6 a	
Blend	37.1 a	4.9 a	19.3 a	7.8 b	3.2 a	3.7 a	51.7 ab	25.1 a	28.5 a	9.5 a	65.2 a	
2000												
Control	25.3 b	5.4 c	20.5 b	12.7 a	4.7 a	3.5 a	55.0 b	36.8 a	37.8 a	16.7 a	89.4 a	3.7 a
Urea	31.7 a	5.9 b	21.0 b	10.0 b	3.9 b	3.4 a	61.8 a	32.6 a	34.2 b	18.1 a	80.0 b	4.4 a
Blend	31.9 a	7.0 a	22.4 a	8.9 c	3.7 b	3.6 a	60.5 a	33.5 a	32.4 b	19.6 a	80.5 b	4.7 a
2001												
Control	25.3 b	2.6 c	14.8 ab	9.5 a	3.8 a	3.2 a	60.7 a	47.2 a	32.6 a	10.1 a	95.4 a	6.4 a
Urea	28.2 a	2.8 b	14.6 b	8.5 b	3.5 b	2.9 b	58.7 a	40.7 b	29.3 a	10.1 a	81.7 b	4.2 a
Blend	27.5 a	3.2 a	15.5 a	8.3 b	3.5 b	2.9 b	56.0 a	44.2 ab	29.8 a	9.4 a	79.5 b	4.1 a

[a]Means ($n=45$) within each year followed by the same letter are not significantly different ($P\leqslant 0.05$).

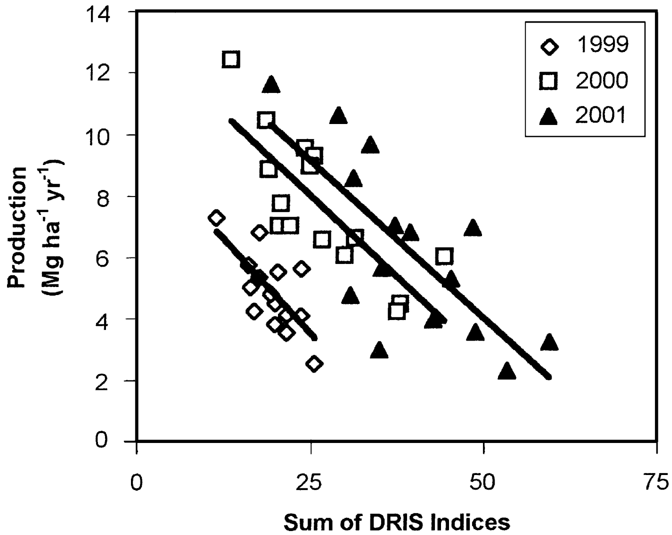

Fig. 2. Aboveground biomass production plotted against the sum of DRIS indices for three treatment years. In 1999, the least squares regression equation was $y = -0.24x + 9.56$ ($r^2 = 0.51$), in 2000 it was $y = -0.21x + 13.2$ ($r^2 = 0.64$), and in 2001 it was $y = -0.20x + 14.1$ ($r^2 = 0.55$). Each point is the treatment average at each experimental location ($n = 3$).

3.3. Leaf and canopy responses

Leaf and canopy characteristics were affected by year, treatment and site factors. Individual leaf area, weight and specific leaf area all responded similarly to each of these factors. Individual leaf area is an example (Table 6). As with productivity, individual leaf area responded to both fertilization treatments and there were no differences between the effects of urea and blend treatments. There were site-to-site differences in individual leaf area. Leaves at Barth averaged $127 \pm 5\,\mathrm{cm}^2$ whereas leaves at Fore and Hofstad averaged 105 ± 7 and $102 \pm 7\,\mathrm{cm}^2$, respectively. There were no treatment-by-site interactions (Table 3).

Much of the site-to-site variation in leaf size in 2001 resulted from the forest tent caterpillar infestation. At Barth, where insecticide was applied, upper canopy leaves averaged 29% smaller in 2001 than in 2000. In 2001, leaves at Hofstad and Fore averaged 53% of the 2000 size. Sampling was done after pupation and subsequent re-foliation, but insect damage decreased the average size less at Barth than other locations.

Leaf litter also showed a fertilizer treatment response. Litterfall was significantly greater with fertilizer treatments than in the control (Table 6). Litterfall was not different between urea and blend treatments. Overall differences in the amount of litterfall among sites were also apparent. DN17 at Barth had the greatest average litterfall ($2.62 \pm 0.12\,\mathrm{Mg\,ha^{-1}}$, $n = 27$), while DN17 at Hofstad had the lowest average litterfall ($1.68 \pm 0.09\,\mathrm{Mg\,ha^{-1}}$, $n = 27$). We attributed some of the site-to-site differences in leaf litter to forest tent caterpillar infestation and control measures taken at Barth. The average amount of leaf litter collected at Barth declined 3% from 2000 to 2001, while that collected at the other sites declined 28% from 2000 to 2001.

Table 6
Average leaf and canopy characteristics for stands grown with three fertilizer treatments

	Oct 1999	Oct 2000	Oct 2001
Individual leaf area (cm^2)			
Control	106 ± 6 b[a]	118 ± 5 b	74 ± 5 b
Urea	127 ± 5 a	150 ± 6 a	81 ± 6 ab
Blend	120 ± 5 a	158 ± 5 a	85 ± 8 a
Litter ($\mathrm{Mg\,ha^{-2}}$)			
Control	1.7 ± 0.1 b	2.2 ± 0.1 b	1.6 ± 0.1 b
Urea	2.2 ± 0.1 a	2.7 ± 0.2 a	2.4 ± 0.2 a
Blend	2.0 ± 0.1 ab	2.6 ± 0.1 a	2.2 ± 0.2 a

Means $\pm$ standard error include values for replicate plots at five study sites ($n = 15$).
[a]Means ($n = 15$) within each year followed by the same letter are not significantly different ($P \leqslant 0.05$).

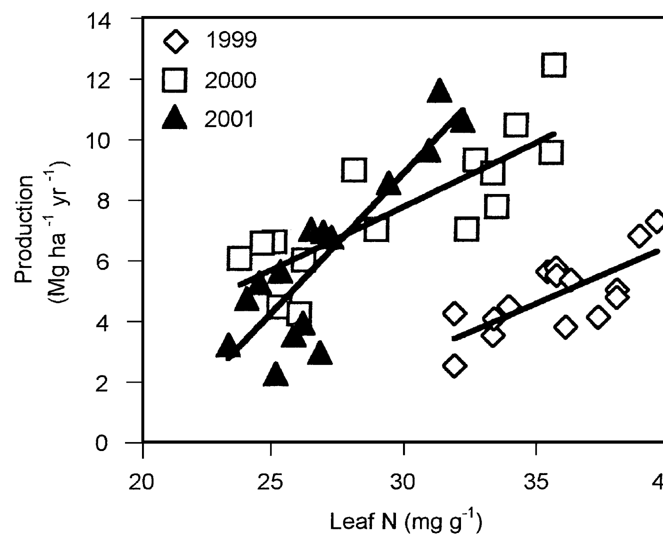

Fig. 3. Aboveground biomass production in response to leaf nitrogen (N) concentration for three years of treatment. In 1999, the least squares regression equation was $y = 3.8x - 8.5$ ($r^2 = 0.53$), in 2000 it was $y = 4.2x - 4.8$ ($r^2 = 0.66$), and in 2001 it was $y = 9.5x - 19.3$ ($r^2 = 0.75$). Each point is the treatment average at each experimental location ($n = 3$).

3.4. Nitrogen and growth efficiency

The fact that similar responses were observed for productivity, N content, and leaf litter suggests interrelationships among them. Fig. 3 shows a significant correlation between leaf N concentration and aboveground production within each year ($P < 0.0001$). Differences among the slopes of annual lines indicate that increases in leaf N concentration resulted in a greater increase in production in 2001 than in earlier years. Treatment had no effect on the relationship between leaf N concentration and aboveground production ($P = 0.31$).

There was also a strong correlation between leaf litter and aboveground production ($P<0.0001$). This relationship differed by both year and by treatment ($P<0.01$). Fig. 4 shows year-to-year differences in these relationships. The slope of the line increased in successive years. Growth efficiency, expressed as production divided by leaf area index [23], was calculated for each plot based on leaf litter mass and specific leaf area. Fig. 5 shows that growth efficiency of the blend treatment was significantly greater than that of the controls in each year, but growth efficiency for the urea treatment was not greater than the control except in 2000.

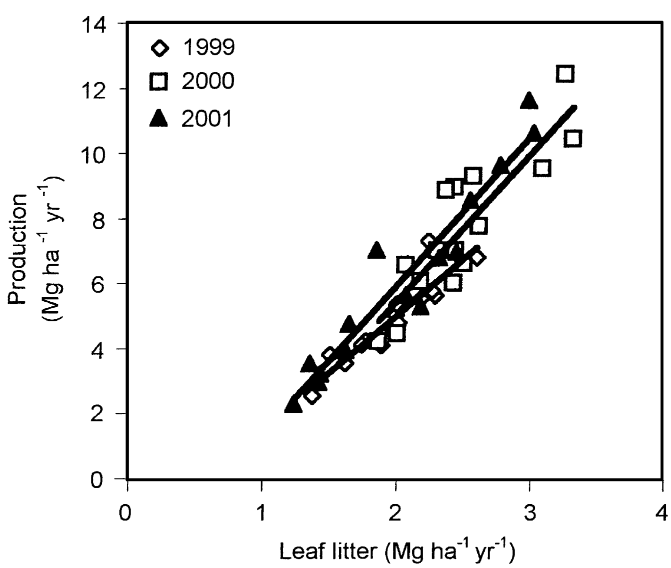

Fig. 4. Aboveground biomass production plotted in response to leaf litter production for three years of treatment and observation. In 1999, least squares regression equation was $y = 3.5x - 2.0$ ($r^2 = 0.83$), in 2000 it was $y = 4.6x - 3.7$ ($r^2 = 0.77$), and in 2001 it was $y = 4.6x - 3.3$ ($r^2 = 0.92$). Points are treatment averages at each experimental location ($n = 3$).

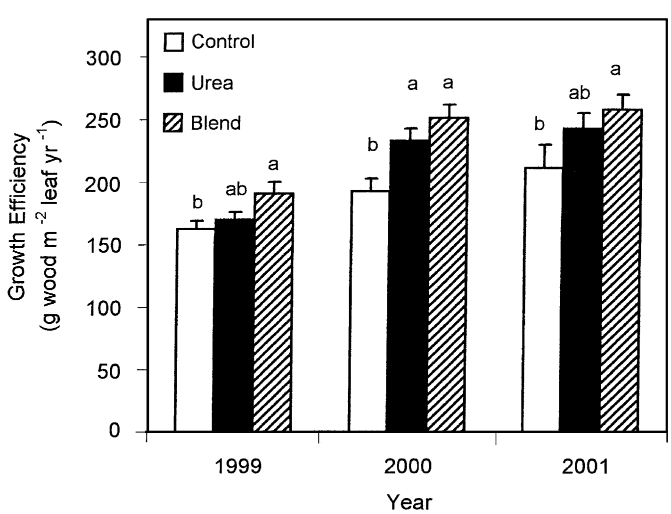

Fig. 5. Annual fertilizer treatment effects on growth efficiency. Each bar is the mean $\pm$ se ($n = 15$). Bars are not significantly different within each year if they have the same letter ($\alpha = 0.05$).

4. Discussion

Aboveground biomass production in these hybrid poplar plantations was limited by nutrient availability. Fertilization resulted in significant responses during the first year, and the response increased in each successive year of treatment (Table 2, Fig. 1). By the end of the third year, biomass was over 40% greater and current annual aboveground production over 80% greater in fertilizer treatments than in the control. Other fertilizer studies with *Populus* at various locations in the US have shown production increases ranging from 21% to 62% [3–7].

Fertilizer responses were consistently positive, although production rates varied from site to site. Fertilizer treatment effects were expected to vary from site to site, because of variable soil, genotype and cultural conditions [8,27,30]. Consistently positive fertilizer responses at all sites suggest that increased growth can be expected on these soil types from annual fertilizer applications initiated near the canopy closure stage of stand development.

The large response of production to fertilizer amendments was not predicted based on initial leaf N concentrations. In 1999, leaf N concentrations were well above the $30\,mg\,g^{-1}$ sufficiency levels [9]. Control leaf N concentrations did drop to $25\,mg\,g^{-1}$ by 2000. Decline of N concentrations with increasing plantation age suggests that a single critical N level will not adequately describe nutrient requirements for all stages that a single development. Nitrogen demand is highest at the time of canopy closure and declines thereafter [9]. Our study began at or just prior to this peak in N demand. The positive response observed at all study sites, despite high leaf N concentrations, demonstrates that significant and consistent responses to N amendments can be expected in stands at this stage of development even when leaf concentrations exceed the critical level.

Our results suggest that the sufficiency level concept does not portray temporal changes of nutrient requirement during stand development. Reliance on the $30\,mg\,g^{-1}$ sufficiency level to predict nutrient requirement of these stands would have missed an opportunity to increase production through fertilization. Delaying fertilizer application until foliage concentrations dipped below deficiency levels may have missed the most responsive stage of stand development. Rather than relying on a single sufficiency level, growers may be more successful by identifying the most responsive growth stage and scheduling fertilization at that time. If diagnostic criteria are to be used to customize application rates for individual sites it will require development of age-specific sufficiency levels.

4.1. Leaf N vs. production

Leaf N concentration was positively correlated with aboveground production when data were separated by year of observation (Fig. 3). In younger plantations with higher N concentrations, there was a lower response of production to a given change in N concentration than in older plantations. Hansen and Tolsted [8] observed a similar linear relationship between production and leaf N concentration and Hansen et al. [30] also observed an increase in the slope of the relationship with age. The change in the slope of this relationship from year to year may be caused by inherent developmental effects or by nutrient limitations as inter-tree competition increases over time. Nutrient availability is typically higher for establishing stands and declines with increased competition [31]. Production declines may also reverse with fertilization [32], which suggests that time effects are influenced more by site nutrient dynamics than by inherent developmental controls.

The linear increase of production with N concentration is consistent with results of nutrient addition experiments. Growth and nutrient concentration are known to be correlated with the rate of nutrient additions in *Populus* and other species grown in controlled environments and field studies [8,10,11,33–35]. Our annual fertilizer applications were designed to mimic addition rate experiments. High-dose fertilizer applications commonly used in forestry result in greater leaching loss and lower fertilizer use efficiency than do split applications [36]. Internal concentrations peak during the year of a single high-dose amendment. In later years, high initial concentrations decrease [37]. Annual applications maintain internal nutrient concentrations and sustain productivity. In our study, the response to fertilization actually increased with multiple applications. Similar increased growth responses were observed in hybrid poplar by Hansen et al. [30] for responsive soil types, and have been observed in many other forest types [33]. Our results indicate that annual granular fertilizer application will serve to increase nutrient concentrations, and cause a linear production increase.

The linear relationship between leaf N concentration and production in response to multiple low-dose fertilizer amendments also indicates limits to the critical-level diagnostic approach. Our data do not show a threshold concentration beyond which no further increases in production occur. Although such a limit likely exists, it is not obvious in Fig. 3 or in the findings of Hansen and Tolsted [8]. The linear relationship observed here suggests that stand managers should strive to achieve the highest concentrations possible, providing DRIS ratios remain balanced. The greater sensitivity of production to leaf N concentration in later years suggests that maintaining high foliar N concentrations will provide even greater gains as plantations age. Furthermore, striving to simply maintain artificial critical nutrient concentrations may limit potential fertilizer response and impede achievement of optimal production.

4.2. Growth efficiency

Growth efficiency increased in response to fertilizer treatments and in older trees (Figs. 4 and 5). Growth efficiency has been shown to increase with both fertilization and age in a range of forest types [24–26,32,38,39]. However, observations in plantations near the end of rotation show that growth efficiency can decrease with age. Greater age-related decline in fertilized plots than in unfertilized plots is likely due to nutrient limitations [32,38]. The increase in growth efficiency with age in our poplar stands was enhanced by fertilization, and this suggests that nutrient amendments at this point in the rotation will yield optimal response. Our observations occurred during canopy closure, when inter-tree competition would be less severe than later in the rotation.

4.3. Nutrient balance

The nutritionally balanced blend treatment did not produce a greater response than that obtained with the N-only urea treatment. The lack of additional response indicates either that no other nutrient added in the blend treatment was limiting growth on this site or that the amounts of other nutrients applied in the blend were inadequate to stimulate a response. The latter possibility is unlikely because other nutrients were applied in ratios favorable for poplar [10,40]. The tissue concentrations of many macronutrients increased in response to both urea and blend treatments, and tissue concentrations of those micronutrients that declined in response to urea treatments remained at sufficient levels. Soils in this region appear to be well supplied with all nutrients required for tree growth except N.

DRIS indices indicate that the trees were in favorable nutrient balance prior to receiving nutrient amendments (Table 5). Levels of Mg were more imbalanced than those of the other nutrients included in DRIS analysis. Supra-optimal levels of Mg were found, especially in older trees. Other nutrients were well within ± 10 units of zero, the balance level. Both the urea treatment and the blended fertilizer treatment resulted in improved nutrient balance for each of the elements. The lower sum of DRIS indices demonstrates the impact of fertilization on improving nutritional balance. Favorable balance of the DRIS indices is further evidence that no other nutrients were deficient on these sites, and that N-only fertilizer amendments will result in sustainable increases in production. However there were instructive patterns in the relationship between DRIS index sums and production.

Nutritional balance declined with age as shown by increasing index sums in successive years (Table 5 and Fig. 2). Reasons for this imbalance in DRIS indices may include uptake imbalance and internal redistribution imbalance. Fig. 2 shows that the observed range of DRIS indices was correlated with a threefold change in production, which suggests that management activities should strive to keep the sum of DRIS indices as low as possible. Keeping the sum to near zero will optimize nutrition and maximize production. The intercept for the regression lines presented in Fig. 2 predicts that maximum potential aboveground production at these locations is 10, 13, and $14\,Mg\,ha^{-1}$ in years 1999, 2000, and 2001. Nutrition programs aimed at optimizing nutrition using these nutrient balance diagnostic tools will increase production much more than those focused on critical levels for leaf nitrogen.

Recommendations for achieving optimal nutrition resulting from this project include:

(1) Initiate N amendments at or just prior to canopy closure where demand is expected to be highest.
(2) Apply small annual doses to maintain internal leaf N concentrations at the highest levels achievable while avoiding lost from the site.
(3) Maintain optimal nutritional balance by minimizing DRIS index sums.

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